
A REVIEW OF THE GENUS *PYROSTEGIA* (BIGNONIACEAE)^{1,2}

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ABSTRACT

Pyrostegia C. Presl is a genus of four species in the tribe Bignonieae. All the species are lianas with compound leaves with two leaflets and a terminal tendril, campanulate calyces, narrow corollas with lobes valvate basally in bud, four exerted stamens, compressed, linear capsules that dehisce parallel to the septum, and thin, bialate seeds. Three of the species are apparently hummingbird pollinated and have flowers that are very similar in appearance with red-orange (rarely yellow), narrow tubular-infundibular corollas. The fourth species, which is probably moth pollinated, has strongly fragrant, white, salverform corollas. All four species are native to South America. *Pyrostegia venusta* (Ker Gawl.) Miers, a popular ornamental, is cultivated throughout the tropics. Lectotypes are designated for *Bignonia ignea* Vell., *B. tecomiflora* Rusby, *P. cinerea* Bureau ex K. Schum., *P. dichotoma* Miers ex K. Schum., *P. venusta* var. *villosa* Hassl., and *Tynanthus igneus* Barb. Rodr. A key to the species, species descriptions, and a species distribution map are provided, and the relationships of the species are discussed.

Key words: *Arrabidaea*, Bignoniaceae, Bignonieae, hummingbird pollination, *Pyrostegia*.

Pyrostegia C. Presl is a small but diverse genus of four species in the tribe Bignonieae (Bignoniaceae). The genus is native to South America, with *P. venusta* (Ker Gawl.) Miers frequently cultivated throughout the tropics. Like most members of the tribe Bignonieae, *Pyrostegia* species are lianas with the terminal leaflet of their compound leaves usually modified as a tendril, and the fruits dehiscent parallel to the septum. All the species of *Pyrostegia* have stems with multiples of four phloem wedges (Santos, 1995), leaves with two leaflets and a terminal tendril, calyces campanulate with five minute denticules, fairly narrow, moderately thick-textured corollas with the narrow lobes valvate at their bases in bud, four exerted stamens, compressed, linear capsules, and thin, bialate seeds. Three of the species are apparently hummingbird pollinated and have flowers that are very similar in appearance: red-orange (rarely yellow), narrow tubular-infundibular corollas with the stamens inserted below the middle of the corolla tube. However, two of these species (*P. dichotoma* Miers ex K. Schum. and *P. venusta*) have nodes with glandular fields absent, tendrils apically trifid, and the corolla tubes externally glabrous, while the third species (*P. cinerea* Bureau ex K. Schum.) has nodes

with glandular fields present, simple tendrils, and densely pubescent corolla tubes. The presence or absence of interpetiolar glandular fields is a useful character in recognizing genera in the Bignonieae (Sandwith, 1938; Seibert, 1948; Gentry, 1993) and has frequently been used as a generic criterion. However, Gentry (1980) warned that the presence of interpetiolar glandular fields can be variable even within a species and should not be used alone as an absolute generic character. Similarly, leaf tendrils can be an extremely useful generic character, with some genera having only simple tendrils, while other genera have only trifid tendrils (Urban, 1916; Gentry, 1993). However, there are genera and even species where both types of tendrils are found (Gentry, 1980), so again, this character should not be used as an absolute in defining genera. Finally, corolla pubescence can also be an important character for differentiating genera (Gentry, 1980) and is frequently employed in keys to genera (Sandwith, 1938; Gentry, 1982), but again, it can be variable within a genus. Nonetheless, retaining *P. cinerea* within the genus *Pyrostegia* is somewhat suspect, and alternative placement is discussed in the taxonomy section of this paper. The fourth species in the genus (*P. millingtonioides* Sand-

¹This paper is number 14 of the Gentry Invitation Series, in acknowledgment of the contributions to the study of the Bignoniaceae made by Alwyn H. Gentry.

²I thank the staff of the following herbaria for providing loans of herbarium specimens: AAU, B, BM, BR, C, CAS, CM, F, FTG, G, GH, GOET, L, M, MICH, NY, S, TEX, U, UPS, US, W and Timothy Harris, Peter Phillipson, and Lúcia Lohmann for providing digitized images. I thank W. D. Stevens and Lúcia Lohmann for their advice and helpful comments on the manuscript, Bee Gunn for preparing the plant illustrations, and Duan Bills for help in preparing the species distribution map. I give particular thanks to the technical staff at the Missouri Botanical Garden whose work made the specimens available for study and who entered a large percentage of the specimens into the TROPICOS database. Financial support was provided by the National Science Foundation (grant 57298).

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doi: 10.3417/2003090

with) has nodes with glandular fields absent, tendrils apically trifid, and the corolla tubes externally glabrous, but has flowers that are quite different in appearance from the other three species. It has strongly fragrant, white, salverform corollas with stamens inserted near the mouth of the corolla tube and is probably moth pollinated. Gentry (1990a: 125) found that switches from one pollinator to another within a genus are relatively rare and suggested that "such changes appear mostly to be associated with major genetic reorganization that accompanies generic differentiation." Placement of *P. millingtonioides* is discussed in more detail in the taxonomy section of this paper.

HISTORY

C. Presl established the genus *Pyrostegia* (Presl, 1845). He provided a thorough description of the genus and the type species, *Bignonia ignea* Vell. (= *P. venusta*), which he transferred into his new genus. However, he made no mention of the aestivation of the corolla lobes, a character made much of by other authors. De Candolle (1845) had treated *B. ignea* as a synonym of *B. venusta* Ker Gawl., placing emphasis in his description on the valvate aestivation of the corolla lobes. Miers (1863: 188) also emphasized the corolla lobe aestivation, describing the lobes as "almost valvate in aestivation, a feature quite peculiar to the genus." Miers (1863) transferred *B. venusta* and *B. longiflora* Cav. to *Pyrostegia* and listed 10 additional names as new species, but did not provide descriptions for the new taxa. Schumann (1894) established the new genus *Macranthisiphon* Bureau ex K. Schum., into which he transferred *B. longiflora*. Monotypic, *Macranthisiphon* is similar to most of the species of *Pyrostegia* in having narrow, orange-red corollas with narrow corolla lobes and exerted stamens; it differs in the corolla lobes being imbricate and in having large foliaceous pseudostipules. Schumann (1894) also published two more species of *Pyrostegia*, *P. cinerea* and *P. dichotoma*, in his treatment of Bignoniaceae for *Die Natürlichen Pflanzenfamilien*, and used the valvate aestivation of the corolla lobes as an early lead in his key to genera in the tribe Bignonieae. In their treatment of Bignoniaceae for *Flora Brasiliensis*, Bureau and Schumann (1896, 1897), treated *P. ignea* (Vell.) C. Presl as a synonym of *P. venusta*, added the new species *P. tubulosa* Bureau & K. Schum. (= *P. dichotoma*), and again emphasized the valvate aestivation of the corolla lobes by using this character to separate *Pyrostegia* and *Glaziova* Bureau from other genera of the Bignonieae with 3(2, 1)-foliolate leaves, filiform tendrils, and floral discs. Urban (1916) transferred *B. tecomiflora* Rusby (= *P. dichotoma*)

to *Pyrostegia*. Sandwith added *P. millingtonioides* to the genus and, while commenting that his new species was unusual in the genus both in corolla color and shape and in the level of insertion of the stamens, nonetheless expressed that it could be placed in this genus "with some confidence" (Sandwith, 1962: 465). This was the last addition to the genus. Macbride (1961) placed *P. dichotoma* in synonymy with *P. venusta* in the *Flora of Peru*, but Gentry (1982) recognized the two as close but separate species in his treatment of Bignoniaceae for the *Flora de Venezuela*.

ANATOMY

Santos (1995) studied 31 genera of Bignonieae and divided them into four groups based on the type of cambial variant. Three species of *Pyrostegia*, *P. cinerea*, *P. dichotoma*, and *P. millingtonioides*, were included in her study. *Pyrostegia* falls into her group 2, which is characterized by possession of stems with multiples of four phloem wedges. Santos found all the genera in her group 2 to be so similar that it was difficult to separate them anatomically. All the genera in this group were found to have septate fibers, cylindrical stems and absence or rare occurrence of perforated ray cells, and scanty to vascicentric paratracheal parenchyma. Other genera in group 2 are *Amphilophium* Kunth, *Anemopaegma* Mart. ex Meisn., *Clytostoma* Miers ex Bureau, *Cydista* Miers, *Distictis* Mart. ex Meisn., *Haplolophium* Cham., *Mansoa* DC., *Mussatia* Bureau ex Baill., *Periarrabidaea* A. Samp., *Phryganocydia* Mart. ex Bureau, *Roentgenia* Urb., and *Tanaecium* Sw.

PALYNOLOGY

The pollen of *Pyrostegia* is 3-colpate (or sometimes 4-colpate in *P. venusta*) and finely reticulate (Urban, 1916; Sandwith, 1962; Gentry & Tomb, 1979), a pollen type common in the tribe Tecomeae and found in several probably unrelated genera in the Bignonieae (Gentry & Tomb, 1979). Other genera with similar pollen in the Bignonieae include *Roentgenia* (ca. 4-colpate, and exine somewhat warty), *Potamo-ganos* Sandwith, *Stizophyllum* Miers, *Pachyptera* DC. ex Meisn., and some species of *Tanaecium* (Gentry & Tomb, 1979). In *Pyrostegia*, only *P. dichotoma* and *P. venusta* have been examined using SEM (Gentry & Tomb, 1979: fig. 3).

CYTOLOGY

Goldblatt and Gentry (1979) found a base number of $x = 20$ for all but three of the 23 genera of the tribe Bignonieae known cytologically. Their count for

Pyrostegia cinerea (voucher: Gentry 12773) of $2n = 40$ is consistent with this general tribal base number. Joshi and Hardas (1956) reported a count of $3n = 60$ for *P. ignea* (= *P. venusta*) from a non-fruit-setting population cultivated in India. Other species (and populations) of *Pyrostegia* have not been investigated cytologically.

REPRODUCTIVE BIOLOGY

Flowers of *Pyrostegia cinerea*, *P. dichotoma*, and *P. venusta* are typical of those pollinated by hummingbirds: odorless and the corolla usually bright red-orange, of fairly thick texture, with a narrow tube and wider mouth, and more or less glabrous internally (Gentry, 1980, 1990a), while the aromatic flowers of *P. millingtonioides*, with white, narrow, tubular, and thickly textured corollas, are probably moth pollinated (Gentry, 1980, 1990a). Hummingbirds have been reported visiting *P. venusta* (Gobatto-Rodrigues & Stort, 1992; Galetto et al., 1994). Gobatto-Rodrigues and Stort (1992) found *P. venusta* to be self-compatible with facultive outbreeding. The hummingbirds *Eupetomena macroura* Gmelin and *Phaethornis pretrei* Lesson & Delattre were reported as visiting and effectively pollinating *P. venusta*, while a number of insects were found to visit the flowers as nectar or pollen thieves. Galetto et al. (1994) reported the hummingbirds *Chlorostilbon aureoventris* Orbigny & Lafresnaye and *Sappho sparganura* Shaw visiting flowers of *P. venusta*. Their study illustrated the pattern of nectar secretion in *P. venusta*. Gusman and Gottsberger (1996) compared the usual orange-flowered *P. venusta* with the rarer yellow-flowered individuals in respect to floral morphology, nectar composition, carotenoids, and flavenoids, and theorized about how these differences could affect nectar robbing by bees and visits by hummingbirds.

Gentry (1990a) hypothesized that all moth- and hummingbird-pollinated species of Bignoniaceae bloom for a period of several weeks to a few months, building up to a distinct peak of flower production followed by a gradual decrease in number of flowers. He referred to these as cornucopia species. Galetto et al. (1994) and Gobatto-Rodrigues and Stort (1992) confirmed this pattern for the populations of *Pyrostegia venusta* observed in their studies, but with the flowers being produced over a time span of several months (Galetto et al., 1994) or generally for about six months with a two-month peak (Gobatto-Rodrigues & Stort, 1992). This herbarium study did not prove particularly useful in confirming the patterns of phenology. Only two flowering specimens of *P. millingtonioides* were seen, these collected in July and August. Six flowering collections of *P. cinerea*

were observed: May (1), June (2), July (2), and November (1). *Pyrostegia venusta* has been seen in flower throughout the year (except December) but peaks between June and September. *Pyrostegia dichotoma* is more complicated. For its whole range, it has been seen in flower all year, but in Colombia only in January; in Guyana and Suriname in February, September, and October; in Venezuela peaking in March; and in Peru, Bolivia, and Brazil peaking from June to October.

ECONOMIC USES

Pyrostegia venusta is a very popular ornamental, cultivated throughout the tropics. Menninger et al. (1970) included it (as *P. ignea*) on his list of the most beautiful flowering climbers in the world and ranked it as the most popular of all in the tropics.

MATERIALS AND METHODS

Gentry established a private database that compiled label information from herbarium specimens at MO and other herbaria that he examined personally. Gentry's private database has been incorporated into the Missouri Botanical Garden database-management system TROPICOS, <<http://www.tropicos.org/>>, which now contains label information for all *Pyrostegia* specimens housed at MO in addition to those received on loan from AAU, B, BM, BR, C, CAS, CM, F, FTG, G, GH, GOET, L, M, MICH, NY, S, TEX, U, UPS, US, and W. Specimens determined by this author were selected from this database to generate the Index to numbered exsiccatae (Appendix 1) and the distribution maps, the latter with the assistance of Duan Bills. Dots on the maps (Fig. 1) represent a subset of the specimens examined by this author, including specimens with geographic coordinates provided on collection labels and a set of specimens, for which the author estimated the geographic coordinates, selected to illustrate the full geographic range for each species.

TAXONOMIC TREATMENT

Pyrostegia C. Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3: 523. 1845. TYPE: *Pyrostegia ignea* (Vell.) C. Presl [Based on *Bignonia ignea* Vell.].

Lianas; branchlets subangulate with 6 to 8 inconspicuous ribs, lacking, or less frequently with, interpetiolar glandular fields, not lenticular; pseudo-stipules usually inconspicuous, small and subulate. Leaves 2(3)-foliolate, often with a tendril; tendril filiform, apically trifid or less frequently simple, deciduous. Inflorescence a terminal or axillary pani-

cle; bracteoles minute, subulate, and inconspicuous; flowers usually numerous. Flowers with the calyx campanulate, truncate to undulate, the ribs extending apically to form 5 small denticules, these sometimes inconspicuous; corolla narrow tubular-infundibular, moderately thick, red-orange (rarely yellow), and odorless or, less frequently, salverform, thick, white, and fragrant; tube externally glabrous, or less frequently densely pubescent throughout, internally glabrous except at, and sometimes, below the level of insertion of stamens; lobes narrow, $\pm$ valvate at base in bud, pubescent at least along margins; stamens 4, exserted, anthers glabrous, pendulous, dithecal, the thecae subparallel to divaricate; staminode present, small; disc annular-pulvinate; ovary linear-tetragonal, lepidote, bilocular, placentation axile, ovules biseriate in each locule; stigma exserted, broadly, or less frequently, narrowly, bilamellate. Fruit compressed, linear, the valves parallel to the septum, smooth, medial vein sometimes slightly raised; seeds thin, bialate, wings brown with hyaline margins.

KEY TO SPECIES OF *PYROSTEGIA*

- 1. Corollas white, narrowly salverform, ca. 3 mm wide at mouth of tube, lobes elliptic-oblong, at least 1/2 as wide as long, 0.6–0.7 cm long; stamen filaments 0.15–0.2 cm long; interpetiolar ridge present . . .
..... 3. *P. millingtonioides*
- 1'. Corollas red-orange (rarely yellow), narrowly tubular-infundibular, 6–13 mm wide at mouth of tube, lobes oblong, less than 1/2 as wide as long, 1–1.8 cm long; stamen filaments 2.6–5.5 cm long; interpetiolar ridge absent.
- 2. Corolla tube externally densely red-puberulent; leaflets with pubescence densely silvery- or ferruginous-tomentose, adaxially glabrescent; tendrils simple; interpetiolar glandular fields present; stigma lobes subulate 1. *P. cinerea*
- 2'. Corolla tube externally glabrous; leaflets glabrous to densely short-pilose; tendrils apically trifid; interpetiolar glandular fields absent; stigma lobes orbicular, ovate, or broadly oblong.
- 3. Staminodes inserted at same level as stamens (rarely to 0.4 cm above insertion of stamens); inflorescence trichomes minute, appressed to ascending; inflorescence generally open; mature fruits generally drying brown to dark brown
..... 2. *P. dichotoma*
- 3'. Staminodes inserted (rarely 0.8) 1.2–1.6 cm above insertion of stamens; inflorescence trichomes longer, initiating at right angles to surface; inflorescence generally crowded with calyces overlapping in dried specimens; mature fruits generally drying with olive cast 4. *P. venusta*

1. *Pyrostegia cinerea* Bureau ex K. Schum. in Engl., Nat. Pflanzenfam. 4(3b): 223. 1894. TYPE: Brazil. Minas Gerais [cultivated at Rio de Janeiro: Quinta da Boa Vista], s.d. [28 Feb. 1882], A. Glazion 14124 (lectotype, designated here, P [barcode P00481542] not seen, P digitized image!; duplicates, P [barcode P00481543] not seen, P digitized image!, C!, photo F neg. 22143!).

Tynanthus igneus Barb. Rodr., Vellozia, ed. 2, 1: 50, 3: ser. 2: tab. 10. 1891, non *Pyrostegia ignea* (Vell.) C. Presl, 1845. TYPE: Brazil. Amazonas: “Arvensis ad ripas Rio Negro, prope Manaos,” ser. 2, tab. 10 in Barbosa Rodrigues, Vellozia, ed. 2, vol. 3 (lectotype, designated here, tab. 10 in Barbosa Rodrigues, 1891b!).

Branchlets silvery- to ferruginous-tomentose, interpetiolar glandular fields present, interpetiolar ridge absent. Leaves 2-foliolate with a simple terminal tendril; petioles 0.5–2.2 cm, tomentose; petiolules 0.5–1.2 cm; leaflets oblong or ovate, subinequilateral, 4–12.5 $\times$ 2.5–6.5 cm, membranous, 4 or 5 pairs of lateral veins prominent below, silvery- to ferruginous-tomentose and adaxial surface eventually glabrescent, scattered pellucid-lepidote, base rounded, apex acute-mucronulate or briefly acuminate-mucronulate. Panicle terminal or terminal and axillary, narrowly elongate with calyces not overlapping in dried specimens, 1 to 3 times branched, peduncle, rachis, and bracteoles silvery- to ferruginous-tomentose; calyx excluding denticules 4–5 $\times$ 4–5 mm at apex, silvery- to ferruginous-tomentose, occasionally with few lepidote scales; corolla narrow tubular-infundibular, orange (rarely yellow); tube 2.5–3.5 cm long, 2.4–3 mm wide at base, 7–10 mm wide at mouth, internally sericeous at and below insertion of stamens, externally densely red-puberulent; lobes oblong, 1–1.5 $\times$ 0.3–0.4 cm, internally red-puberulent apically and marginally, externally densely red-puberulent; stamens and staminode inserted at approximately same level in corolla tube, 1–1.2 cm from base of tube, stamen filaments 2.7–3.2 cm, thecae porrect-divaricate, 2.3–3 mm, staminode 6–12 mm; disc 1.2–2 $\times$ 1.2–2 mm; pistil 4–5.5 cm, ovary 2–2.8 $\times$ 0.6–1 mm, stigma lobes subulate. Capsule 17.5–19 $\times$ 0.9–1 cm, glabrous, drying brown, midvein slightly raised, base and apex acute; seeds 0.7–0.9 $\times$ 2.2–2.5 cm (Fig. 2C–F).

Distribution. Brazil, disturbed areas or campinas (white sand areas) near Manaus, State of Amazonas, presumably at low elevations (Fig. 1).

Phenology. Flowering May to July and November; fruiting November.

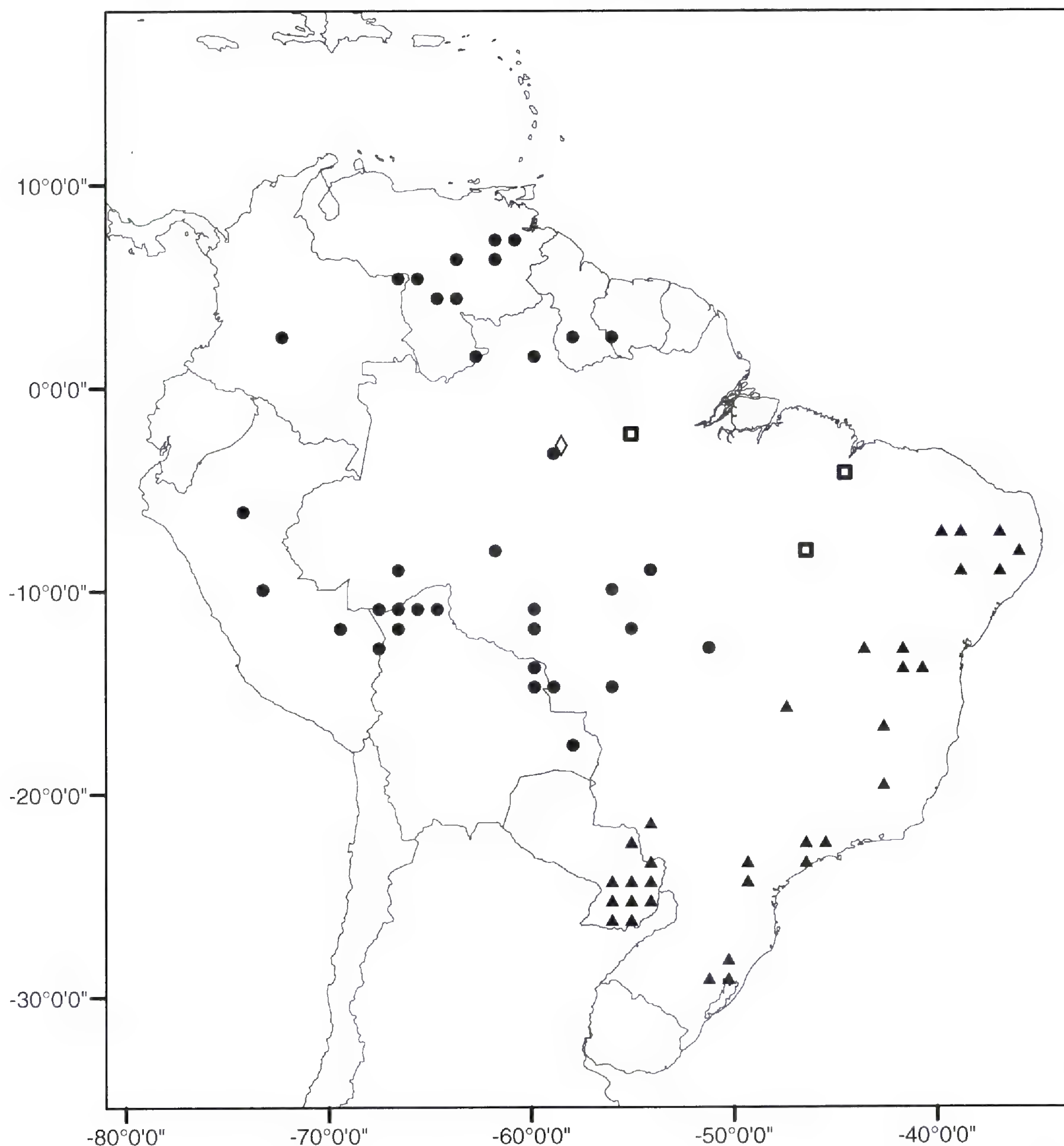


Figure 1. Distribution of species of *Pyrostegia*, excluding cultivated and apparently naturalized specimens. *Pyrostegia cinerea* Bureau ex K. Schum. (◇), *P. dichotoma* Miers ex K. Schum. (●), *P. millingtonioides* Sandwith (□), and *P. venusta* (Ker Gawl.) Miers (▲).

Discussion. Schumann (1894) published *Pyrostegia cinerea* Bureau ex K. Schum. in his key to *Pyrostegia* without any indication of type collection. It is assumed here that the species was included in Schumann's key based on information from Bureau and that the type collection was at P. Two collections at P are annotated in what I believe to be Bureau's handwriting. A. *Glaziou 14124* (barcode P00481542) is annotated by Bureau as "Nouveau," and with potential specific epithets (*discolor* and *cinerascens*) with a line drawn through them and finally "*cinerea* α *discolor*." *Jobert 452* is annotated by Bureau as

"*Pyrostegia cinerea* n. sp. β *concolor*." The *Glaziou* collection is chosen here as the lectotype in part because I suspect that Bureau would have been more likely to indicate the type variety as variety α versus variety β, and because duplicates of *Glaziou 14124* are extant; in fact the sheet at C also seems to be annotated in Bureau's hand. Unfortunately, while *P. cinerea* is endemic to Amazonas, Brazil, the lectotype is labeled as from Minas Gerais. However, *Glaziou* is known to have changed localities (and sometimes also the collector, collection number, and/or date of collection) on some specimens (Wurdack, 1970).



Figure 2. A, B. *Pyrostegia millingtonioides* Sandwith (from G. S. Pinheiro 19, MO). —A. Flower bud. —B. Longitudinal section of corolla with androecium, style, and stigma. C–F. *Pyrostegia cinerea* Bureau ex K. Schum. (from A. Ducke 532, MO). —C. Flowering branch. —D. Stem node with glandular field. —E. Style and stigma. —F. Longitudinal section of corolla with androecium.

The duplicate of *A. Glaziou 14124* at C is without locality information. The second collection of *A. Glaziou 14124* at P (barcode P00481543) is labeled as made from cultivated material at Quinta da Boa Vista, Rio de Janeiro, collected 28 Feb. 1882. Glaziou (1911) reports both his numbers *14124* and *19666* (the latter cited by Bureau & Schumann, 1897, as *19665*, from Minas Gerais) as cultivated at Quinta da Boa Vista, S. Christovão, Rio de Janeiro. It is therefore assumed that the lectotype *A. Glaziou 14124* (barcode P00481542), while labeled Minas Gerais, is a duplicate of *A. Glaziou 14124* (barcode P00481543), and was made from cultivated material at Quinta da Boa Vista, Rio de Janeiro. *A. Glaziou 14124* (barcode P00481543) is not a lectotype candidate as it was formerly in Glaziou's private herbarium, not donated to P until 1907, and not annotated by Bureau.

According to Stapf (1909: 225), Barbosa Rodrigues made his descriptions and illustrations from living plants with an “almost complete absence of specimens.” Stafleu and Cowan (1983: 829) were unable to locate any types or other herbarium specimens of Barbosa Rodrigues and concluded that the most important protologue materials for Barbosa Rodrigues' new taxa were to be found in his published and unpublished drawings. Barbosa Rodrigues' excellent plate, ser. 2, tab. 10 (Barbosa Rodrigues, 1891b) is thus chosen here as the lectotype of *Tynanthus igneus*. The quality of the illustration and description leave no doubt that *T. igneus* is synonymous with *Pyrostegia cinerea*, a conclusion previously reached by Bureau and Schumann (1896: 198). While *T. igneus* Barb. Rodr. (Barbosa Rodrigues, 1891a) has priority over *P. cinerea* Bureau ex K. Schum. (1894), *P. ignea* (Vell.) C. Presl (1845) blocks the transfer of the Barbosa Rodrigues name to *Pyrostegia*.

The simple tendrils, interpetiolar glandular fields, and externally pubescent corollas of this species are unexpected in the genus *Pyrostegia*, where they are otherwise not known (Fig. 2C, D). These characters suggest an affinity with the genus *Arrabidaea* DC. Sandwith (1968: 405–406) established a set of characters, which when found in combination, could suggest inclusion in the genus *Arrabidaea*: “branchlets terete or subterete, not definitely tetragonous; tendrils simple; corolla tomentose outside, at least on the limb, nearly always pink, purple or white, very rarely creamy yellow, never full yellow; disk conspicuous; anther thecae parallel, divergent or divaricate, glabrous, not curved or contorted; pollen-grains simple, 3-furrowed; ovary oblong; ovules 2 to 4 seriate in each loculus; capsule narrow, linear-oblong, compressed. Glandfields may be present or absent at the nodes, though commonly present; trichomes of the

indumentum may be short and simple, long and multicellular, sometimes gland-tipped, or branched and ‘dendroid’ (sometimes forming a dense fur), but not stellate; the foliage in two species is for the most part bipinnately 2–3 ternate; foliaceous pseudostipules are rarely, but sometimes present; the inflorescence is often a pyramidal thyrse, but may be short and axillary and is sometimes found on the old wood; the calyx is extraordinarily variable in shape, size and texture, and in the presence or absence of teeth or lobes; the corolla varies from hypocratifform in species with very small flowers to campanulate-funnelshaped in most of those with larger flowers; the stamens are usually included but in one species the anthers are conspicuously exserted; the capsule is usually smooth, but in two widely distributed species is densely prickly-tuberculate; the seeds usually have membranous wings, but in certain water-borne species are wholly corky.” *Pyrostegia cinerea* differs from this typical picture of *Arrabidaea* in its large, orange, narrow tubular-infundibular corolla and exserted stamens. Sandwith's concept of *Arrabidaea* included no species with true yellow or orange corollas; however, *A. elegans* (Vell.) A. H. Gentry does have yellow to orange corollas, though Gentry (1975) suggests that this and *A. bilabiata* (Sprague) Sandwith might be better placed in a separate genus. *Arrabidaea lauta* Bureau & K. Schum. is very similar to *P. cinerea* and was initially placed in *Pyrostegia* by Miers (1863). Not only is it similar florally, with a pubescent, narrow tubular-infundibular corolla with oblong lobes and exserted stamens, but it is also similar vegetatively, with interpetiolar glandular fields and 2-foliolate leaves with a simple tendril. This might suggest that *A. lauta* would fit more comfortably in the genus *Pyrostegia*, rather than supporting a relationship between *P. cinerea* and the genus *Arrabidaea*. However, *A. lauta* differs from species of *Pyrostegia* in the imbricate aestivation of its corolla lobes, more delicately textured, red corolla, strongly recurved anther thecae, and relatively broader calyx. The pollen of *P. cinerea* was examined by Urban (1916) using light microscopy and found to be more similar to that of *P. dichotoma* and *P. venusta*, that is, 3(or 4)-colpate and finely reticulate (Gentry & Tomb, 1979), than to species of *Arrabidaea*, 3-colpate and more or less psilate or smooth (Gentry & Tomb, 1979). Anatomically, *P. cinerea* fits well with the other two species of *Pyrostegia* examined (Santos, 1995) into Santos' (1995) group 2, characterized by stems with multiples of four phloem wedges in transverse section. Species of *Arrabidaea* belong to Santos' (1995) group 1, characterized by stems with only four phloem wedges in transverse section. Crystals were found in the vessels of most of the species of

Arrabidaea examined, but not in any of the species of *Pyrostegia*.

Pyrostegia cinerea is maintained for the time being in *Pyrostegia* primarily on the basis of the corolla lobe aestivation, valvate for the basal half to two thirds. This appears to be an unusual character state in the Bignoniaceae. The narrow tubular-infundibular corolla shape found in *Pyrostegia* appears to have evolved repeatedly in the family and in the tribe Bignonieae in groups pollinated by hummingbirds (Gentry, 1974, 1980); however, this does not seem to be true of the corolla lobe aestivation. Gentry (1990a) lists the following genera of the Bignonieae as strictly hummingbird pollinated: *Dolichandra* Cham., *Fridericia* Mart., *Gardnerodoxa* Sandwith, *Macranthisiphon*, *Martinella* Baill., and *Piriadacus* Pichon. All of these have the corolla lobes clearly imbricate in bud.

Additional specimens examined. BRAZIL. Northern Brazil, *Jobert 452* (P not seen, P digitized image). **Amazonas:** Manaus, C. A. W. Schwacke III-278 (GOET); Manaus, Ig. da Cachoeira Baixa do Tarumã, J. Chagas s.n. INPA-1198 (U); Estrada de Aleixo, NE Manaus, ca. 10 km to Leper Colony, A. Lasseigne P22582 (MO); along Aleixo-rd., P. J. Maas & H. Maas 326 (MO); outskirts of Manaus, rd. to INPA, A. H. Gentry 12857 (MO); Manaus, loco Estrada do Aleixo, A. Ducke 532 (MO), 532-II (US); grounds of INPA at Manaus, A. H. Gentry & G. T. Prance 11198 (MO); vic. of Manaus rd. toward Rio Negro, 10 km N from Manaus on Estrada Aleixo, A. H. Gentry et al. 12773 (MO); Km 14 on Estrada Mauá, G. T. Prance & Prance 21012 (NY); Reserva Florestal Ducke, Manaus-Itacoatiara, Km 26, Floresta de Campinarana, L. G. Lohmann et al. 34 (MO). **Rio de Janeiro:** [Cultivated at Quinta da Boa Vista, S. Christovão], A. Glaziou 19666 (C, P not seen, P digitized image).

2. *Pyrostegia dichotoma* Miers ex K. Schum. in Engl., Nat. Pflanzenfam. 4(3b): 223. 1894. TYPE: Peru. San Martín: Tarapoto, 1855–1856, R. Spruce 3930 (lectotype, designated here, G!, photo F neg. 26203!; isotypes, BM!, BR!, G-DC not seen, GH!, K not seen, NY!, P not seen, W!).

Bignonia tecomiflora Rusby, Mem. Torrey Bot. Club 6: 101. 1896, "tecomaeiflora." *Pyrostegia tecomiflora* (Rusby) K. Schum. ex Urb., Ber. Deutsch. Bot. Ges. 34: 746. 1916. TYPE: Bolivia. La Paz: Mapiri, July–Aug. 1892, M. Bang 1510 (lectotype, designated here, NY [barcode 278056]!; duplicates, A!, BM!, MICH!, MO!, NY [barcode 564088]!, US!).

Branchlets sparsely lepidote and/or sparsely to densely covered with small curved-ascending to appressed trichomes, or glabrous, interpetiolar glandular fields absent, interpetiolar ridge absent. Leaves 2-foliolate, often with an apically trifid terminal tendril, or leaves 3-foliolate; petioles 1.5–4 cm, with curving trichomes in adaxial canal; petiolules 0.5–3 cm; leaflets ovate, slightly subinequilateral, 2.5–12 × 1.4–6.7 cm, chartaceous (membranous), 3 to 5 pairs of lateral veins prominent abaxially, sometimes

with trichomes along midvein on adaxial surface and/or at base of abaxial surface, pellucid-lepidote, often especially conspicuous abaxially, with large glands in the axils of lower lateral veins, base rounded or truncate, apex acuminate-mucronulate or briefly acuminate-mucronulate. Panicle usually terminal, sometimes axillary, open with calyces not overlapping in dried specimens, 2 to 4 times branched, peduncle, rachis, and bracteoles nearly glabrous to densely covered with minute, ascending-curved to appressed trichomes, sometimes also lepidote; calyx excluding denticles 4.5–8 × 4.5–10 mm at apex, with sparse lepidote scales, sometimes minutely puberulent, apex ciliate; corolla narrow tubular-infundibular, orange or reddish orange; tube 3.5–7 cm long, 3–5 mm wide at base, 6–13 mm wide at mouth, internally sericeous at and below insertion of stamens, externally glabrous; lobes oblong, 1–1.8 × 0.3–0.6 cm, puberulent apically and marginally, externally sometimes lepidote; stamens and staminode inserted at approximately same level in corolla tube (or staminode up to 4 mm above higher stamens), 1–3 cm from base of tube, stamen filaments 3.6–5.5 cm, thecae slightly divergent or subparallel, 3–4.5 mm, staminode (sometimes developing an anther) 2–25 mm; disc 1.5–2 × 2–3 mm; pistil 5–7 cm, ovary 3–7 × 1 mm, stigma lobes ovate, broadly ovate, or broadly oblong. Capsule (rarely 11) 18–33 × 0.8–1.2 cm, glabrous, drying brown, midvein apparent but not conspicuous, base acute, apex aristate; seeds 0.6–1 × 2.6–4.5 cm (Fig. 3C–F; Gentry, 1982: fig. 38).

Distribution. Guyana, Suriname, Venezuela, Colombia, Peru, Bolivia, and Amazonian Brazil; 30–1500 m elevation, generally found below 1000 m. It is frequently reported to be found in disturbed areas, in savannas with islands of larger trees, or in dry, moist, or wet forest. The soil type is often described as sandy (Fig. 1).

Phenology. For whole range, flowering and fruiting throughout year. In Colombia flowering in January; in Guyana and Suriname in February, September, and October; in Venezuela peaking in March; and in Peru, Bolivia, and Brazil peaking from June to October.

Common names. Venezuela: Barqui (Gentry, 1982), Tango (*Xena* 257); Peru: Paccha huasca (*Ferreya* 5070); Bolivia: Lluvio de Oro (*Guillén et al.* 4108).

Discussion. Miers (1863) published the name *Pyrostegia dichotoma*, without description, citing one collection, *Spruce 3930* from Tarapota [Peru]. Schumann (1894: 223) validly published *P. dichotoma* without directly specifying the type or any collections, but by citing "*Pyrostegia dichotoma* Miers aust Ostperu," indirectly indicated *Spruce 3930* as the

type. Bureau and Schumann (1897) cite the same collection as the only specimen of *P. dichotoma*. A number of specimens of this collection number were seen from a variety of herbaria (BM, BR, G, GH, NY, W, also at G-DC, K, and P, but these not seen), and it is assumed that Schumann also had a specimen at B, and that specimen was the holotype and is no longer extant. The specimen at G is chosen here as the lectotype.

When Rusby published *Bignonia tecomiflora*, he was able to base his description upon the complete sets of *Bang 1510* and *1596*. *Bang 1510* (NY, barcode 278056) is selected here as the lectotype based on its excellent condition and completeness: flowers, flower buds, capsules, and seeds are all present on this sheet. Gentry (1982) cited *Pyrostegia tecomiflora* and *B. tecomiflora* as synonyms under both *P. dichotoma* and *P. venusta*. The syntypes of *B. tecomiflora* have the inflorescences more crowded than is generally the case for *P. dichotoma*; however, the type of inflorescence trichomes, minute and appressed, is that generally found in *P. dichotoma* and not found in *P. venusta*. The staminode, in one flower dissected, was at the level of the stamen insertion and, in the other flower dissected, 3 mm above the level of insertion, better fitting the pattern of *P. dichotoma* than *P. venusta*, in which the staminodes are inserted (rarely 0.8) 1.2–1.6 cm above the stamens.

The holotype of *Pyrostegia tubulosa* Bureau & K. Schum. (in Martius, Fl. Bras. 8(2): 231. 1897, *Richard Schomburgk 969*, from Kanuku, Guyana) is presumed to have been at B and destroyed. No isotypes were seen in this study or by Gentry (1982), and none are in the database of Schomburgk collections compiled by The Nationaal Herbarium Nederland (<<http://www.nationaalherbarium.nl/>>). However, three specimens of *Pyrostegia* made in the Kanuku Mountains of Guyana (*Jansen-Jacobs et al. 369*, *437*, and *Wilson-Browne 217*) were studied and not found to be different from other *P. dichotoma*. Bureau and Schumann (1897) used the margin of the calyx, undulate versus truncate, to help separate *P. tubulosa* from *P. dichotoma*. However, the calyx margin is very variable in *P. dichotoma*, and the margin exhibited by the collections from Guyana fit well into that range. Bureau and Schumann (1897) also used the nature of the leaf apex, rostrate versus acuminate to somewhat obtuse, to separate the taxa. The leaf apices of specimens examined from Guyana did not show a significant difference from those of other collections of *P. dichotoma*. The corolla described by Bureau and Schumann (1897), 6.8–7.3 cm long, and that of *Wilson-Browne 217*, 6.5–7 cm long, are larger than those otherwise seen. However, the dissected flower of *Jansen-Jacobs et al. 437* had a total corolla length of

6.2 cm, well within the range for *P. dichotoma*. Based on these observations, *P. tubulosa* is treated here as synonymous with *P. dichotoma* (following Gentry, 1982).

Pyrostegia dichotoma and *P. venusta* are very similar in general appearance. The most reliable way to separate the two is by the level of the staminode insertion. In *P. dichotoma*, the staminode is inserted with the stamens (Fig. 3F), and in *P. venusta*, it is inserted considerably (at least 8 mm) higher in the corolla tube (Fig. 3B). Bureau and Schumann (1897: fig. 98) and Lohmann and Pirani (1998: fig. 10D) provide accurate and useful illustrations of the relative position of the stamens and staminode in *P. venusta*. *Pyrostegia dichotoma* almost always has the inflorescence trichomes minute and appressed to ascending, while in *P. venusta* the trichomes are perpendicular to the surface at least at the base (Fig. 3A). Fabris (1965: fig. 29) provides an excellent illustration of the trichome type found in *P. venusta*. However, it is not uncommon for individuals of both species to have nearly glabrous inflorescences, particularly after the bracteoles have been lost. Additionally, one specimen was seen, *Daly et al. 2271*, which had trichomes of the type generally found in *P. venusta*, but had all the other characteristics of *P. dichotoma*. *Pyrostegia dichotoma* tends to have a more open, often elongate, inflorescence that is 2 to 4 times branched (Fig. 3D; Gentry, 1982: fig. 38), while *P. venusta* generally has a very dense panicle, which is often subcorymbose and either unbranched or 1 or 2 times branched (Bureau & Schumann, 1897: fig. 98; Lohmann & Pirani, 1998: fig. 10A). However, some specimens of *P. venusta*, such as *Yoshiizumi s.n. (ESA-6363)* (from São Paulo, Brazil), *Harley 21606* (from Bahia, Brazil), and *Hassler 11784* (from Central, Paraguay), can have very open inflorescences, while some specimens of *P. dichotoma*, such as *Ducke 725* (from Amazonas, Brazil), *Mathias & Taylor 6080* (from Loreto, Peru), and *Gentry et al. 77514* (from Beni, Bolivia), can have fairly crowded ones. The two species do not appear to be sympatric. While *P. dichotoma* is known from Guyana, Suriname, Venezuela, Colombia, Peru, Bolivia, and Amazonian Brazil, *P. venusta* is native to Atlantic and southern Brazil, from Piauí to Rio Grande do Sul, southern Paraguay, and northeastern Argentina. The latter species is very widely cultivated and possibly naturalizes in some areas.

Selected specimens examined. BOLIVIA. **Beni:** Prov. Vaca Diez, E side of Riberalta, *J. C. Solomon 6148* (MO). **La Paz:** Sorata, *M. Bang 1596* (syntypes of *Bignonia tecomiflora*, A, BM, F, G, K not seen, M, MICH, MO, NY, S, W); Prov. Nor Yungas, Corocoro, 12 km NE of Caranavi, *A. H. Gentry et al. 44347* (MO). **Pando:** Prov. Manuripi, 30 km

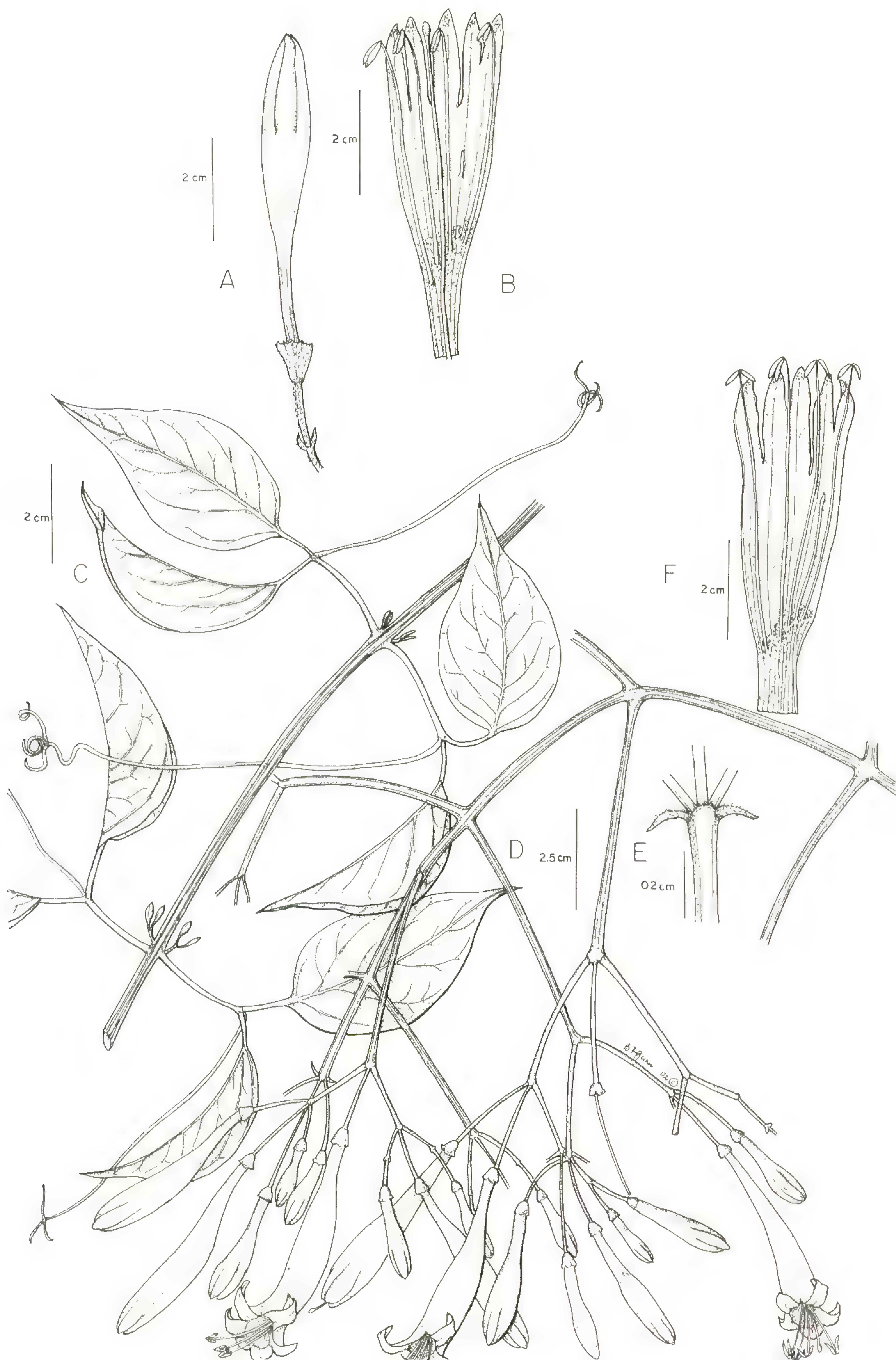


Figure 3. A, B. *Pyrostegia venusta* (Ker Gawl.) Miers (from E. W. Schupp 258, MO). —A. Flower bud. —B. Longitudinal section of corolla with androecium, style, and stigma. C–F. *Pyrostegia dichotoma* Miers ex K. Schum. —C. Branch with tendrillate leaves (from B. Stergios *et al.* 8868, MO). —D. Inflorescence. —E. Inflorescence node (D, E from J. A. Steyermark *et al.* 109875, MO). —F. Longitudinal section of corolla with androecium (from S. F. Smith *et al.* 1051, MO).

N de Puerto America, *A. Jardim et al.* 2431 (MO). **Santa Cruz:** Prov. Velasco, Parq. Nac. Noel Kempff Mercado, Asseradero El Chore, *R. Guillén et al.* 4108 (MO). **BRAZIL.** **Acre:** Mun. de Senador Guimard, BR 317, Km 23, *C. A. Cid & B. Nelson* 2821 (MO). **Amazonas:** Serra near Namorado Novo, watershed betw. Rio Curuquetê and Rio Madeira at Abunã, *G. T. Prance et al.* 14705 (MO). **Mato Grosso:** BR 364, Cuiabá-Porto Velho, Distr. de Patronal, Vila Bela da Santíssima Trindade, *C. A. Cid et al.* 4409 (MO). **Pará:** Near Embrapa station at Km 23 on rd. Altamira-Itaituba, *C. Berg et al.* BG755 (MO). **COLOMBIA.** **Caquetá:** Km 90 on rd. from Neivo to Florencia, ca. 6 km NW of Florencia, *A. H. Gentry et al.* 9067 (MO). **Meta:** Cordillera La Macarena, mesa del Río Sansa, *J. Idrobo et al.* 1274 (MO). **GUYANA.** **Essequibo:** Kanuku Mtns., *M. J. Jansen-Jacobs et al.* 437 (MO). **PERU.** **Loreto:** Pucallpa-Aguaytía rd., Km 37 W of Tournavista, *M. E. Mathias & D. Taylor* 6080 (MO). **Madre de Dios:** Iberia, Río Tahuamanu, *R. J. Seibert* 1952 (MO). **Pasco:** Prov. Oxapampa, Panjil, 12 km by air from Puerto Inca, *D. N. Smith & R. Foster* 2416 (MO). **San Martín:** Prov. San Martín, Tarapoto, *F. Woytkowski* 35089 (MO). **SURINAME.** **Nickerie:** Zuid River, Kayser airstrip, 45 km above confluence with Lucie River, *H. S. Irwin et al.* 57636 (MO). **VENEZUELA.** **Amazonas:** Cerca del pueblo de Macurucu, *P. Berry* 2123 (MO). **Bolívar:** Mun. Sucre, carr. desde Jabillal a Ciudad Bolívar, *E. Sanoja* 2743 (MO). **Delta Amacuro:** Dept. Tucupita, betw. Los Castillos de Guyana and the town of Sierra Imataca, *G. Davidse & A. González* 16437 (MO).

3. *Pyrostegia millingtonioides* Sandwith, Kew Bull. 15: 464. 1962. TYPE: Brazil. Pará: Obidos, in capoeira of terra firme, 23 July 1912, *A. Ducke s.n.* (MG 12046) (holotype, K not seen, K digitized image!; isotype, MG not seen).

Branchlets with dense to scattered curved-ascending trichomes, interpetiolar glandular fields absent, slight interpetiolar ridge present. Leaves 2-foliolate, often with an apically trifid terminal tendril; petioles 1.9–4 cm, with curving trichomes at least in adaxial canal; petiolules 0.5–5 cm; leaflets ovate, slightly subinequilateral, 4–11 × 2–6 cm, chartaceous, 3 to 5 pairs of lateral veins prominent abaxially, both surfaces densely to sparsely pilose to pilose only on veins or glabrous, pellucid-lepidote, often especially conspicuous abaxially, with large glands in the axils of lateral veins, base rounded or truncate, apex briefly acuminate-mucronulate, or acuminate-mucronulate. Panicle terminal, densely corymbose or paniculate with calyces overlapping in dried specimens, 2 to 4 times branched, peduncle, rachis, and bracteoles covered with minute, ascending-curved to appressed trichomes; calyx excluding denticles 3–4.5 × 5.5–6 mm at apex, with sparse lepidote scales, sometimes minutely puberulent, apex ciliate; corolla narrowly salverform, white; tube 4.1–5.5 cm long, 2–2.3 mm wide at base, ca. 3 mm wide at mouth, internally glabrous or pubescent near mouth, externally glabrous; lobes elliptic-oblong, 0.6–0.7 × ca. 0.4 cm, puberulent apically and marginally; stamens and

staminode inserted at approximately same level in corolla tube, 3.9–4.4 cm from base of tube, stamen filaments 0.15–0.20 cm, thecae subparallel, 1.7–2 mm, staminode ca. 1 mm; disc 1.5–1.75 × ca. 1 mm; pistil ca. 4.4 cm, ovary 2–3 × ca. 0.8 mm, stigma lobes reniform-suborbicular. Fruit not known (Fig. 2A, B).

Distribution. Brazil, in the states of Pará and Maranhão; in dry secondary growth; elevation not recorded on labels (Fig. 1).

Phenology. Flowering in July and August.

Discussion. This species, with its strongly fragrant, white, salverform corollas, and stamens inserted near the mouth of the corolla tube, seems oddly placed in *Pyrostegia*, which otherwise has probably odorless (Gentry, 1990a), orange, narrow tubular-infundibular corollas with the stamens inserted below the middle of the corolla tube. *Pyrostegia cinerea*, *P. dichotoma*, and *P. venusta* are typical of hummingbird-pollinated Bignoniaceae flowers: odorless, the corolla bright red-orange (or deep red-violet), of fairly thick texture, with a narrow tube and wider mouth, and more or less glabrous internally (Gentry, 1980, 1990a), while the fragrant flowers of *P. millingtonioides*, with white, narrow, tubular, and thickly textured corollas, are probably moth pollinated (Gentry, 1980, 1990a). Gentry (1990a) reported that change of pollinator within a genus of Bignoniaceae is very rare and that only 18% of the Neotropical genera of Bignoniaceae have more than one type of pollen vector, and most of the species in these genera are overwhelmingly bee pollinated with one or two species switching to hummingbird pollination. Only two other genera of Neotropical Bignoniaceae, *Arrabidaea* and *Tabebuia* Gomes ex DC., have both moth- and hummingbird-pollinated species, and most of the species in those two genera are bee pollinated (Gentry, 1990a). *Pyrostegia* is the only genus reported (Gentry, 1990a) to have both hummingbird- and moth-pollinated species, with no species pollinated by bees.

On the other hand, there may be a positive correlation between dry habitats (such as that of *Pyrostegia millingtonioides*) and moth pollination. In a comparison of pollinators of lianas in different types of forests, Gentry (1991) suggested that a larger percentage of hummingbird-pollinated species is found in moist and wet forests (2%) or pluvial forests (7%) than in dry forests (1%), and a larger percentage of moth-pollinated species is found in dry forests (2%) versus moist and wet forests (0%) and pluvial forests (1%).

The insertion of the stamens above the middle of the corolla tube appears to be associated with the moth-pollinated syndrome. Gentry (1990a) listed three

genera in the Bignoniaceae as exclusively moth pollinated: *Tanaecium*, *Leucocalantha* Barb. Rodr., and *Sphingiphila* A. H. Gentry (listed as new genus). *Leucocalantha* (pers. obs.), *Tanaecium* (Macbride, 1961), and *Sphingiphila* (Gentry, 1990b) all have the stamens inserted above the middle of the corolla tube. Therefore, the main differences between *Pyrostegia millingtonioides* and *P. dichotoma* and *P. venusta* appear to be associated with pollen vector. The three species have many morphological characters in common: absence of interpetiolar glands, presence of generally 2-foliolate leaves with an apically trifid tendril, leaflets similar in shape and indument, calyx of similar shape, corolla tubes glabrous externally, corolla lobes more or less valvate at base in bud, stamens and stigma exerted, and a relatively wide stigma. In addition, as previously discussed, the pollen of all four species of *Pyrostegia* is 3(or 4)-collate and finely reticulate (Urban, 1916; Sandwith, 1962; Gentry & Tomb, 1979), and *P. millingtonioides*, *P. dichotoma*, and *P. cinerea* have similar wood anatomy (Santos, 1995). Alternative generic placement of *P. millingtonioides* is not suggested at this time.

Additional specimens examined. BRAZIL. **Maranhão:** Rodovia Açailândia–Santa Inês, Km 100, G. S. Pinheiro 19 (MO); St. Luzia, Reserva Florestal de Buriticupu, propriedade da Floresta Rio Doce S.A. 52 km de Buriticupu, G. dos Santos et al. 41 (MO), 42 (MO). **Pará:** Obidos, A. Ducke s.n. (RB 16322) (NY).

4. *Pyrostegia venusta* (Ker Gawl.) Miers, Proc. Roy. Hort. Soc. London 3: 188. 1863. Basionym: *Bignonia venusta* Ker Gawl., Bot. Reg. 3: tab. 249. 1818. *Tecoma venusta* (Ker Gawl.) Lem., Hort. Universel 5: 1. 1843. TYPE: tab. 249, illustration of greenhouse plant cultivated at Combe Wood, England, from seed originally from Rio de Janeiro, Brazil (lectotype, designated by Sandwith & Hunt, 1974: 75, tab. 249 in Ker Gawler, 1818!).

Bignonia ignea Vell., Fl. Flumin. 244. 1825 [1829]. *Pyrostegia ignea* (Vell.) C. Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3: 523. 1845. TYPE: tab. 15 in Vellozo, Fl. Flumin. Icones 6. 1827 [1831] (lectotype, designated here, tab. 15 in Vellozo, 1827 [1831]!).

Pyrostegia venusta var. *villosa* Hassl. in Sprague, Bull. Herb. Boissier, sér. 2, 5: 84. 1905 [1904]. TYPE: Paraguay. Capibary, Dec., E. Hassler 5940 (lectotype, designated here, G!; duplicates, A!, BM!, K not seen. MO!, NY!, S!, W!).

Branchlets glabrous, or with few trichomes at the nodes, or scattered to densely short-pilose to puberulent, interpetiolar glandular fields absent, interpetiolar ridge absent. Leaves 2-foliolate, often with an apically trifid terminal tendril (the ends rarely branched again, bifid or trifid), or leaves 3-foliolate;

petioles 1–4 cm, densely pubescent, pilose in the adaxial canal or glabrous; petiolules 0.4–3 cm; leaflets ovate (rarely lanceolate), slightly subinequilateral, 2.5–11.5 × 1.2–6 cm, chartaceous (rarely membranous), 3 to 5 pairs of lateral veins prominent below, densely short-pilose to glabrous, pellucid-lepidote, often especially conspicuous abaxially, with large glands in the axils of lower lateral veins, base rounded or truncate (rarely cordate), apex briefly acuminate-mucronulate, or acuminate-mucronulate (obtusely-mucronulate or acuminate). Panicle usually terminal or axillary, generally dense or subcorymbose with calyces often overlapping in dried specimens, unbranched or 1 or 2 (rarely 3) times branched, peduncle, rachis, and bracteoles nearly glabrous to densely puberulent or pilose, the trichomes initially perpendicular to the surface; calyx excluding denticules 4–8 × 4.5–10 mm at apex, with sparse lepidote scales, glabrous to densely short-pilose to puberulent, apex ciliate; corolla narrow tubular-infundibular, orange or reddish orange (rarely yellow); tube (rarely 2.7) 4–7 cm long, 2–5 mm wide at base, 8–13 mm wide at mouth, internally sericeous at and below insertion of stamens and staminode, externally glabrous; lobes oblong, 1–1.8 × 0.3–0.7 cm, puberulent apically and marginally; stamens inserted 1.3–3.5 cm from base of corolla tube, staminode inserted (rarely 0.8) 1.2–1.6 cm above insertion of higher stamens, stamen filaments (rarely 2.6) 3.2–5.2 cm, thecae subparallel, (rarely 3) 4–6.3 mm, staminode 1–8 mm (rarely developing an anther and then similar in length to, and inserted with, stamens); disc 1–3 × 2–3 mm; pistil 4.6–8.5 cm, ovary 4–6.5 × ca. 1 mm, stigma lobes broadly ovate, ovate, orbicular, or broadly oblong. Capsule 13.5–30 × 0.8–1.5 cm, glabrous, drying with olive cast, midvein apparent, but not conspicuous, base acute, apex aristate; seeds 0.7–1.4 × 2.8–4.5 cm (Fig. 3A, B; Fabris, 1965: fig. 29; Bureau & Schumann, 1897: fig. 98; Lohmann & Pirani, 1998: fig. 10A–E).

Distribution. Atlantic and southern Brazil, from Piauí to Rio Grande do Sul, southern Paraguay, and northeastern Argentina; 70–1300 m elevation, generally found below 1000 m. Frequently reported as growing in disturbed semi-evergreen forest or cerrado. Cultivated as an ornamental throughout the tropics and subtropics and possibly naturalizing in some areas (Fig. 1).

Phenology. Collected in flower in every month except December, peaking June to September. Fruiting July to December.

Common names. Brazil: Cipó de São João (Sandwith & Hunt, 1974; Heringer 1982), Cipó Caititu

(Cutler 8404), Cipó Tingá (*Carauta* 408), Dedo de Moça (*Emperaire & Campelo* 2748); Argentina: Pico de Tucán, Flor de San Juan (Fabris, 1965); Peru: Lluvia de Oro (*Seibert* 2333); Guatemala: Chiltote, Chorro de Oro, Chorro (Standley & Williams, 1974); El Salvador: San Carlos (Standley & Williams, 1974); Costa Rica: Triquitraque (Standley & Williams, 1974); U.S.A.: Flame Flower, Flaming-Trumpet, Golden-Shower (Bailey et al., 1976).

Discussion. The Vellozo plate 15 (Vellozo, 1827) was chosen as the lectotype of *Bignonia ignea*, as no Vellozo *Bignonia* specimens have been found (Gentry, 1975). Based on the Vellozo plate and description (Vellozo, 1825), *B. ignea* is placed in synonymy of *Pyrostegia venusta*, following Bureau and Schumann (1897), Sandwith and Hunt (1974), and Gentry (1982).

The six syntypes and 15 of the isosyntypes of *Pyrostegia venusta* var. *villosa* were seen, and *E. Hassler* 5940 (G) is chosen as the lectotype, based on the quality of the specimen and its large number of widely distributed duplicates. Hassler (Sprague, 1905) distinguished *P. venusta* var. *villosa* from the typical variety based strictly on presence or absence of pubescence, the typical variety defined as glabrous to glabrescent and variety *villosa* as the whole plant more or less villous to pubescent. The type material of *P. venusta* var. *villosa* examined in this study had densely pubescent to pilose young branchlets, leaflet surfaces, and pedicels. In this study, specimens with similar pubescence were seen only south of Bahia, Brazil. Plants intermediate in pubescence, that is, with scattered trichomes on the pedicels but with the young branchlet internodes and the leaflet surface between the veins glabrous, were also restricted to this same geographical range. Nearly all specimens throughout the entire species range showed some degree of pubescence, with at least some trichomes present in the adaxial canals of the petioles and petiolules and on the bracteoles of the inflorescence. The trichomes are of the same type as those found on the more pubescent specimens. The less pubescent plants are found throughout the entire range of the species and, in fact, appear to grow in the same localities as the pubescent individuals. For example, the following pairs of pubescent and less pubescent plants were collected at the same localities and on the same dates: *Zardini* 14343 and *Zardini* 14365 and *Zardini* 7193 and *Zardini* 7131. It seems more appropriate at this point not to formally recognize the variety.

Pyrostegia dichotoma has been treated as a synonym of *P. venusta* by some authors (Macbride, 1961). The two are treated here as separate but closely related species, as discussed below *P. dichotoma*.

Menninger et al. (1970) includes *Pyrostegia ignea* (= *P. venusta*) on his list of the most beautiful flowering climbers in the world, and ranks it as the most popular of all in the tropics. It is very widely cultivated and possibly naturalizes in some areas (Gentry, 1973). The specimen *Ferreira* 192 indicated that the plant is considered toxic to cattle and has been used as a tonic and anti-diarrheic, but I have not seen a published account of this use. *Williams & Assis* 6963 also recorded that the flowers are poisonous to cattle.

Selected specimens examined. ARGENTINA. **Corrientes:** Dep. Ituzaingó, Isla Apipé Grande, Panco-cué, A. Schinini & R. Vanni 15813 (MO). BRAZIL. **Bahia:** Mun. de Mucuri, 14–17 km a W de Mucuri, S. A. Mori et al. 10423 (MO); ca. 45 km N of Santa Maria de Vitória, on rd. to Serra Dourada, R. M. Harley et al. 21606 (MO). **Ceará:** Serra de Araripe, near entrance to rd. to Novo Exu, H. C. Cutler 8404 (MO). **Minas Gerais:** Mun. de Marliéria, Parque Estadual do Rio Doce, E. P. Heringer 13984 (MO). **Paraíba:** Mun. de Maturéia, Pico do Jabre, Serra de Teixeira, M. F. Agra 4398 (MO). **Paraná:** Faz. Água dos Índios (Cianorte), G. Hatschbach 21599 (MO). **São Paulo:** Santa Genebra Forest Reserve, Barão Geraldo, near Campinas, A. H. Gentry 59074 (MO). PARAGUAY. Atira, E. Hassler 3022 (syntype of *Pyrostegia venusta* var. *villosa*, G; isosyntypes, A, BM, K not seen, NY, W), 3022-a (syntype of *Pyrostegia venusta* var. *villosa*, G; isosyntypes, K not seen, NY); Cholulu, E. Hassler 6663 (syntype of *Pyrostegia venusta* var. *villosa*, G); Ipe-hu, E. Hassler 5244 (syntype of *Pyrostegia venusta* var. *villosa*, G; isosyntypes, BM, NY, W); Concepcion, E. Hassler 7363 (syntype of *Pyrostegia venusta* var. *villosa*, G; isosyntype, NY). **Caaguazu:** 103 km E of Coronel Oviedo on rd. to Puente Strossner, A. H. Gentry 59440 (MO). **Guairá:** Cordillera de Ybytyruzú, 15 km N of Atena on rd. Melgarejo–Atena, E. Zardini & R. Velásquez 13555 (MO). **Itapúa:** Pirapó, CEDEFO, W. Hahn & L. Pérez de Molas 2760 (MO). **San Pedro:** 12 km al NE de Choré, E. Zardini & C. Benítez 3401 (MO).

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APPENDIX 1. Index to Exsiccatae. Collections are alphabetical by collector name. After the collector's number, the number in parentheses corresponds to the species number in the List of Species. Type collections appear in boldface. All collections cited here were examined by this author as part of this study.

LIST OF SPECIES

1. *Pyrostegia cinerea* Bureau ex K. Schum.
2. *Pyrostegia dichotoma* Miers ex K. Schum.
3. *Pyrostegia millingtonioides* Sandwith
4. *Pyrostegia venusta* (Ker Gawl.) Miers.

Ackermann s.n. (4). *Agostini* 1501 (2). *Agra et al.* 1955 (4), 4398 (4), 4480 (4). *Aguayo* 117 (4), 303 (4), 562 (4), 594 (4). *Aguilar* 217 (4). *Alston* 6402 (4). *Amaral et al.* 1165 (2). *Anderson* 72 (4). *Andrade et al.* 214 (4), 229 (4). *Andrade-Lima & Lima* 39 (4). *Angeli* 358 (4). *Annable* 2823 (4). *Araujo* 384 (4). *Arbo et al.* 2267 (4), 2656 (4). *Arenas* 1181 (4). *Arroyo et al.* 730 (2). *Aymard et al.* 6303 (2), 7582 (2), 7587 (2), 7618 (2).

Bahia 100 (2). *Balansa* 488 (4). *Balapure* 656 (4). *Ball s.n.* (4). *Bang* **1510 (2)**, **1596 (2)**. *Barreto* 787 (4), 790 (4). *Barth* 1233 (4). *Basualdo* 709 (4), 1032 (4), 1556 (4). *Basualdo s.n.* (4). *Belanger* 204 (4). *Belém* 1163 (4), 1554 (4), 1603 (4), 3876 (4). *Belshaw* 3431 (2). *Berg et al.* BG755 (2). *Berl* 1477 (4). *A. L. Bernardi* 19584 (4). *L. Bernardi* 18049 (4). *Berry* 1654 (2), 2123 (2). *Bertoni* 861 (4), 1477 (4), 2801 (4), 3744 (4), 3772 (4). *Billiet & Jadin* 3351 (4). *Blanchet* 2563 (4). *Boom* 9777 (4). *Boone* 1240 (4). *Bowie & Cunningham s.n.* (4). *Breedlove* 23552 (4). *Brenes* 23234-A (4). *Bright* 4099 (4), 4100 (4). *N. L. Britton & E. G. Britton* 9289 (4). *Brunner et al.* 914 (4). *Buchtien* 1314 (2). *Bunting & Dios Holmquist* 4613 (2), 4618 (2). *Burchell* 4768 (4).

- Cabral* 34 (4). *Cabrera & Sáenz* 29226 (4). *Cadial & Watkiss* 73 (2). *C. E. Calderon et al.* 2765 (2), 2835 (2). *S. Calderón* 573 (4). *Camargo* 1634 (4), 2156 (4). *Cambar* 199 (4). *Capelosa* 7 (4). *Carauta* 408 (4), 854 (4), 871 (4), 888 (4). *Carauta et al.* 4738 (4). *Cardenas* 2969 (4). *Cardona s.n.* (2). *Carnier* 1140 (4). *Carr s.n.* (2). *Carvalho et al.* 6272 (4). *Castellanos* 23372 (4), 24978 (4). *Castillo* 763 (2). *Catharino* 358 (4). *Pedra do Cavalo* 777 (4). *Chagas s.n. (INPA 1198)* (1). *Chodat* 176 (4), 176-b (4), 177 (4), 178 (4). *Chun* 5489 (4), 6925 (4). *Cid & Nelson* 2821 (2). *Cid et al.* 944 (2), 4409 (2), 4770 (2), 6267 (2), 6278 (2). *Claussen* 66 (4), 188 (4), 190 (4), 489 (4), 8902 (4). *Claussen s.n.* (4). *Coêlho et al. s.n. (INPA 1730)* (2). *Coêlho et al. s.n. (INPA 1738)* (2). *Coradin et al.* 2055 (4), 5724 (4). *J. Cordeiro & Hatschbach* 336 (4). *M. R. Cordeiro* 598 (2). *Cosme* 14(4). *Cristobal & Krapovickas* 1761 (4). *Croizat* 15 (2). *Cutler* 8404 (4).
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